Research Article

Proximity to forest plantations is associated with presence and abundance of invasive plants in landscapes of south-central Chile

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Abstract

Invasive plant species (IPs) are widespread in forests and cause substantial environmental, economic and social impacts. They occupy native ecological niches, causing local extinctions to the detriment of native biodiversity and disrupting ecosystem services provision. How landscape characteristics may determine the success of IPs remains unclear and, more importantly, how land-use and land-cover changes may result in spatial shifts in the invasion risk. Furthermore, the study of how landscape factors may influence biological invasions has focused on particular species, but not the IPs' community. In this study, we identify and assess landscape variables that influence the presence and distribution of the IPs' community in temperate forests of a global biodiversity hotspot in south-central Chile. We fitted spatially explicit models, combining field-sampling information and landscape variables related to land-use/land-cover, topography, climate, soil characteristics and anthropogenic factors to explain and predict the presence and distribution of the IPs' community. From the whole sampling of plant species, we identified eight plant species classified as IPs: three trees and five shrubs. We used field data from 125 500 × 2 m-transects, in which we registered species richness, abundance and basal area of IPs' community. Distance to forest plantations was the landscape variable with the most substantial influence on IPs' presence and distribution. Richness, abundance and basal area of IPs' trees were higher at shorter distances from forest plantations. The basal area of IPs' trees was the best model explaining the relationship between IPs' community and landscape variables. All descriptors of the IPs' community showed similar spatial patterns: species richness, abundance and tree basal area are higher in more disturbed areas. Our findings contribute to increasing our understanding of the distribution patterns of IPs in forest landscapes. Our models can be suitable tools for designing strategies to prevent, mitigate or make integrated control of the impacts of invasive species in forest landscapes.

Key words: Alien plants, basal area, biological invasions, land cover, landscape dynamics, land use

Introduction

Biological invasions might be shaped by landscape characteristics, as landscape structure may influence the patterns of the invasive species community. Anthropogenic landscape alteration plays a fundamental role in explaining the patterns and magnitude of invasions by exotic plants (González-Moreno et al. 2015). This association is mainly mediated by an increase in propagule pressure, the degree of disturbance and habitat connectivity favourable to invasion. Likewise, invasions may shape landscapes, as the invasive species can alter its surrounding environment to make conditions more conducive to its presence (Gouws and Shackleton 2019). For instance, according to Bartuszevige et al. (2006), the landscape structure is of primary importance, while some community attributes, such as disturbance history, canopy openness and woody plant composition, are of secondary importance to determine the invasion risks of the alien shrub *Lonicera maackii*. In this case, the shrub invades from multiple foci (towns) rather than in a frontal advance, independently of the landscape connectivity (i.e. the number of corridors), but depending on edge habitat, probably due to increased propagule pressure. Thus, some of the community attributes associated with *L. maackii* invasion may be indicators of past disturbances.

Invasive plants (IPs) can be considered a particular component in the succession of the plant community. IPs distributions show wide ecological amplitudes, considering they might adapt to different and novel climatic and geographical zones (Thinley et al. 2020). The IPs' presence may be regulated by mechanisms occurring at global scales, but also at local scales of anthropogenic (e.g. social, economic and political) and biophysical variables (Montti et al. 2017). Thus, IPs' invasion risks would depend on the co-occurrence of specific factors at different spatial scales, from global to local. These factors include suitable environmental and climatic conditions, propagule introduction by humans and a posteriori landscape-scale dispersal. For instance, agricultural lands are usually most susceptible to invasion amongst all other land-use types, irrespective of the species (Thinley et al. 2020).

The land-use type may be crucial for shaping the invasion process (Kueffer 2017). Land-use changes related to political processes can create an invasion debt that causes unexpected linkages amongst the invasive plant, native dispersers, land management and topography that, together, can cause cascading changes in ecosystems (Lenda et al. 2018). For instance, the invasion of the alien walnut *Juglans regia* in Poland since 1989 has been a multifaceted process (Lenda et al. 2018). Human-related alterations to propagule pressure biotic and abiotic factors have led to the spread of walnuts from abandoned human settlements and fields to forest ecosystems. Moreover, the changes in land-use and land-cover may result in spatial shifts in the invasion risk (Wang et al. 2016). Although some IPs might not be established in dynamic and heterogeneous landscapes (even with favourable climate conditions), the species may establish when a disturbance such as land-use change occurs (Gillson et al. 2008). The landscape permeability increases, allowing IP colonisation; this produces patchily distributed stands of the same age. Many invasive plants perform better in cleared areas; thus, the connectivity of cleared areas and undisturbed habitat results is critical for their successful colonisation (Green et al. 2006).

Several models represent and predict the dispersion of individual IPs' species considering the characteristics of their natural range, including species distribution

models (Elith 2017). However, few studies have considered the IPs' community to elaborate dispersion or distribution models. Amongst these few studies, we find that of Gong et al. (2020), who used an assemblage-niche-model platform to build niche-based species distribution models and project potential distributions of two invasive plant species (*Cecropia peltata* and *Ulex europaeus*), changes in their distribution under the scenarios of global changes, as well as the underlying mechanisms or factors driving these changes. To assess the status of fish stocks, multispecies virtual population analysis is an attempt to take species interactions; some models treat them as aggregate (continuous) biomass and capture more realistic biological interactions and processes (Gupta et al. 2019). According to Plagányi et al. (2022), multispecies models can reduce bias in parameters, reference points and projections. Multispecies models that cover a wide range of species in the ecosystem span multiple trophic levels from primary producers to top predators. In the context of connectivity conservation plans, they generally develop considering a single species and are rarely empirically evaluated for their relevance to others, limiting our understanding of how connectivity requirements differ between species (Brennan et al. 2020). These same authors recommend evaluating multispecies connectivity to prioritise areas for conservation that safeguard the connectivity needs of multiple species of conservation concern.

Landscape characteristics were one of the most critical drivers for most plant responses in the research about constraints of restoration outcomes across spatial scales of an invasive plant (Rohal et al. 2019). According to their research, the abiotic and landscape variables combined at a patch scale drive the plant community results. Climatic and land-use variables were good predictors of landscape susceptibility to invasion in the south-eastern U.S. (Lázaro-Lobo et al. 2020), especially distance to settlements. Systems anthropogenically perturbed, i.e. developed areas and barren lands were more prone to be invaded. Homogenisation of landscapes through anthropogenic activities (agriculture, forest plantations, urbanisation) helps biotic homogenisation and is a process attributed primarily to the establishment of exotic species (Lobos et al. 2016). Landscape heterogeneity and corridors for propagule dispersal may also increase the landscape susceptibility to invasion for most species (Lázaro-Lobo et al. 2020). The influence of landscape composition and configuration on invasion risk is species-specific. Thus, to better understand the potential impacts of IPs, it is necessary to know the IPs' habitat and the main variables that may facilitate/impede their presence and abundance.

In Chile, 743 species of alien plants have been reported, a higher proportion (15%) than in other Latin American countries (Fuentes et al. 2013). Of these species, over 100 are considered IPs (Fuentes et al. 2014). There is a high concentration of alien species in the South-central region, where practically all IPs at the national level are present. Amongst the causes of this distribution are multiple colonisation waves, higher levels of anthropogenic disturbance, great agricultural and livestock activity and intensification of forest crops in the mid-20th century (Fuentes et al. 2014). The eight species that form the community of IPs in our study area are considered invasive, according to Herrera et al. (2016). *Acacia dealbata* reduces species richness under its understorey, plant cover and seed density, thus modifying the floristic composition, while increasing the coverage of other alien plant species (Herrera et al. 2016). *Acacia melanoxylon* promotes an increase in water-nitrogen concentration and alterations in litter characteristics in native riparian forests, altering the activity and community structure of microbial

decomposers (Pereira et al. 2021). *Eucalyptus globulus* causes alterations of networks of interaction between species of the native community, alters the dynamics of leaf litter-fall, can increase the concentration of soil nitrate, delay the growth of undergrowth plant species and decrease fungal biomass in the river ecosystem (Castro-Díez et al. 2004; Medina-Villar 2016). *Cytisus striatus* is considered a noxious weed in the United States (Ketchum and Rose 2003) and grows aggressively, displacing native species. It increases the risk and intensity of fires and leads the fire to the top of the trees (Fuentes et al. 2014). *Rosa rubiginosa* forms monospecific stands, so, in advanced stages of the invasion, it can impoverish the species composition and alter the structure of affected plant communities (Herrera et al. 2016). It can alter pollination mutualisms by attracting native and exotic pollinators and reducing the reproductive success of native plants. *Rubus ulmifolius* proliferates by colonising open sites, where it prevents the regeneration of native plants, resulting in impoverishment in species composition and altering the structure of affected plant communities (Herrera et al. 2016). It forms impenetrable barriers that limit the circulation of animals and make large areas inaccessible. *Teline monspessulana* creates favourable conditions for fire generation because it tends to form monospecific groupings, it replaces native vegetation, reduces the load capacity of grazing land and increases combustible material (Herrera et al. 2016). *Ulex europaeus* is one of the 100 of the World's Worst Invasive Alien Species (GISD 2021). It is highly competitive, displaces cultivated and native plants and alters soil conditions by fixing nitrogen and acidifying it. *Ulex europaeus* creates an extreme fire hazard due to its oily, highly flammable foliage and seeds and abundant dead material.

Our study provides critical information to understand the relationship between the landscape structure and the IPs in forest landscapes in south-central Chile. Specifically, we: (a) identified and assessed the main landscape variables that influence the presence and distribution of the IPs community and, (b) fitted spatially explicit models to predict the areas with higher IPs' invasion risks. Our proposed model could facilitate early detection and control of IPs, delaying their spread and conserving native flora and fauna, especially in natural protected areas. This research will contribute to our understanding of spatial variation in the key to the success of IPs and control them in the global forests.

Materials and methods

Study area

Our study was conducted in four landscapes of La Araucanía Region in south-central Chile (Fig. 1). These landscapes are in three representative areas of the region: Lumaco (38°18'16"S, 73°05'35"W) in the Coastal-Mountain Range, Freire (38°57'18"S, 72°36'46"W) in the Central Valley and Pucón (39°16'54"S, 71°56'35"W) along with Curarrehue (39°21'28"S, 71°34'59"W) in the Andean-Mountain Range. The two latter contain three natural protected areas: Huerquehue National Park, Villarrica National Park and Villarrica National Reserve (CONAF 2011).

The extension and biophysical characteristics are similar in the four landscapes (Appendix 1: Table A1); however, there are some differences in their main land-use and land-cover types (related to their main economic activities). They constitute a gradient of disturbance, from most disturbed landscapes in the Coastal-Mountain
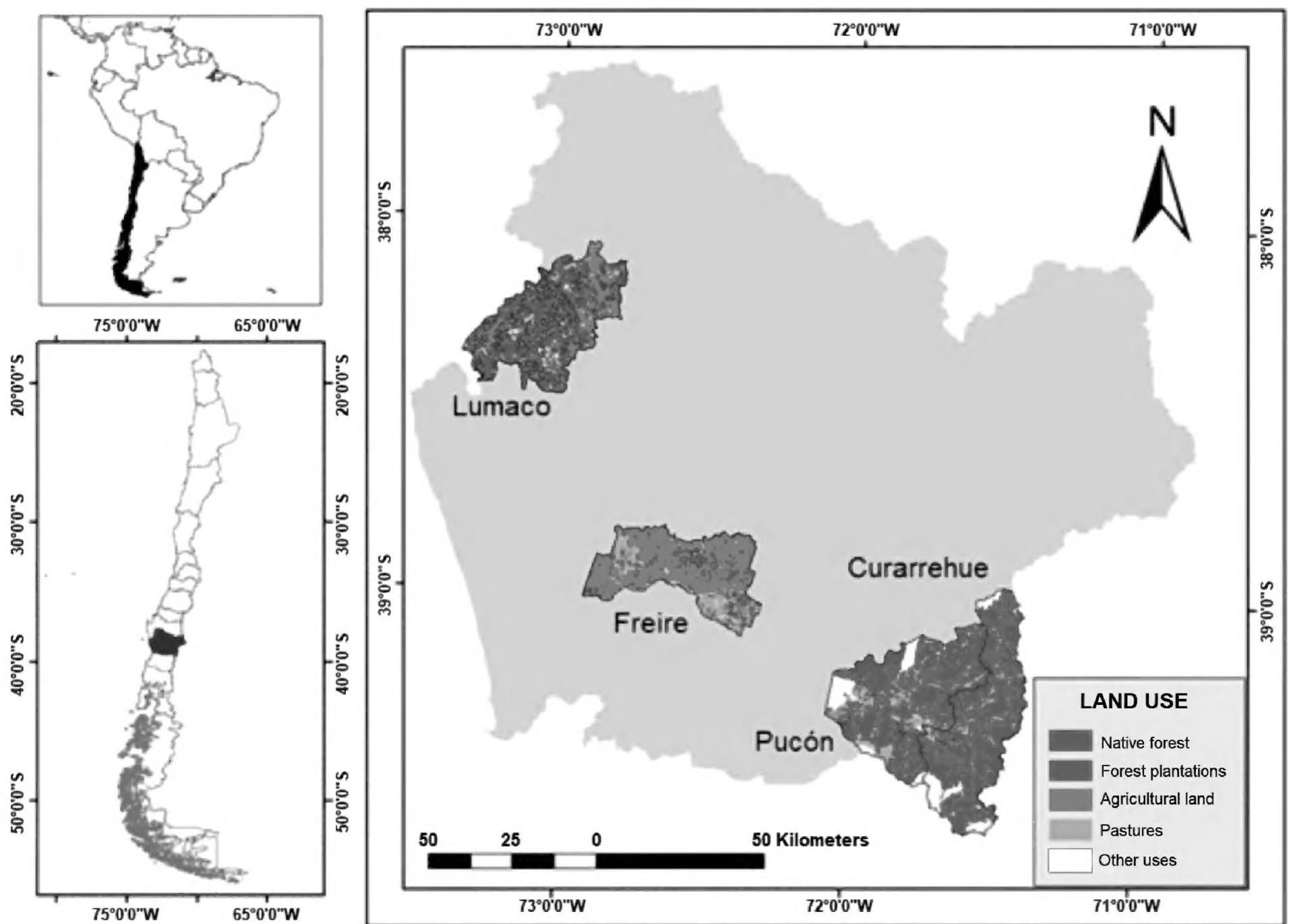
Figure 1. Location of four landscapes in La Araucanía Region, south-central Chile and their main land uses and land covers.

Range (Lumaco) and Central Valley (Freire) to more minor disturbed landscapes near the Andean-Mountains Range (Pucón and Curarrehue) (Altamirano et al. 2020). In Lumaco, forest plantations occupy 64% of the total area, while the remaining native forest only 16% (Fig. 1). In Freire, agricultural lands occupy 62% and native forest only 11%; while in Pucón and Curarrehue, native forests are the primary land use with 71% and 82% of the area, respectively.

The four landscapes are located inside the Chilean hotspot of biodiversity named Chilean Winter Rainfall-Valdivian Forest, which harbours richly endemic flora and fauna (Mittermeier et al. 2011). This hotspot contains 3,893 native vascular plants, of which 1,957 species (50%) are endemic (Arroyo et al. 2006). However, a generalised loss of native forest cover has occurred recently and keeps going, mainly due to conversions to shrublands and exotic forest plantations in some places (Miranda et al. 2017). These forest plantations (exotic species monocultures, mainly *Pinus* and *Eucalyptus*) have dominated large areas of central Chile since the 1990s.

Field sampling

In each landscape, we located 500 × 2 m transects via a random sampling scheme stratified by their main land cover (i.e. native forest, tree plantation, agriculture and pastures) and accessibility. The total number of transects was 125: 31 in Lumaco, 36 in Freire, 30 in Pucón and 28 in Curarrehue (Fig. 2). We identified all
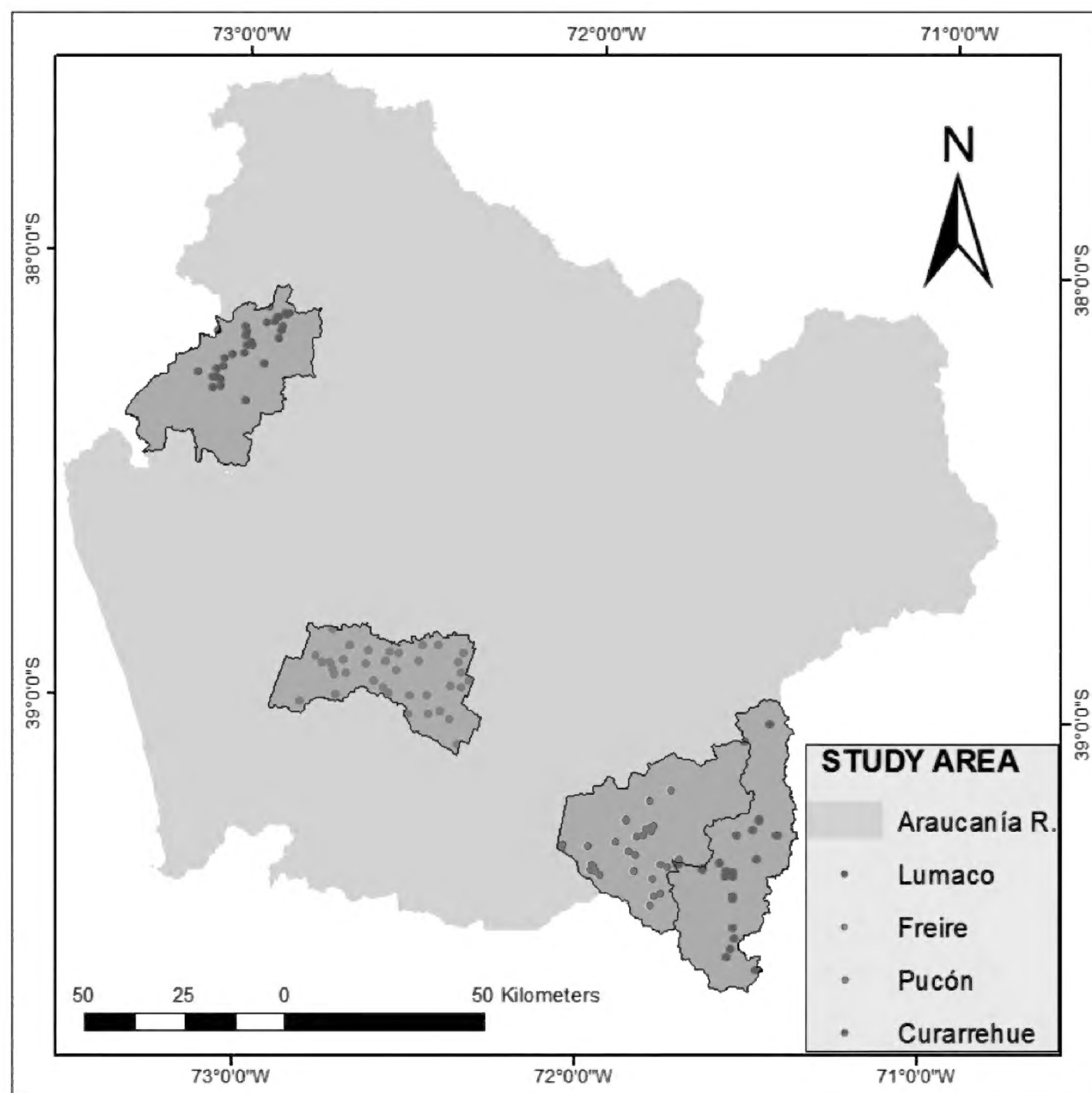
Figure 2. Distribution of 500 × 2 m-transects (n = 125) in four landscapes in south-central Chile. Transects are located via a random sampling scheme stratified by land-use types (see Fig. 1).

trees and shrubs higher than 1.4 m in height to species level in each transect. This height is a good standard metric to register the reality of a moment of the sample, but does not consider smaller, usually younger, plants that could be of great abundance and greater importance in the future. Then, we classified them according to their origin (native or alien) and life form (tree or shrub) and measured their height and diameter at breast height (DBH). We estimated the species richness, trees and shrubs abundance and basal area as potential response variables for those plants registered as IPs to monitor their presence and distribution according to the classification done by Fuentes et al. (2014).

Landscape variables

We extracted a set of landscape variables from spatially-explicit data on climate, topography, soil, and anthropogenic characteristics to obtain the explanatory variables for modelling. We used the climate variables which were obtained from the WorldClim database (www.worldclim.org) and included 19 temperature indicators, rainfall and bioclimatic variables. We derived bioclimatic variables from the monthly temperature and rainfall values to be more biologically meaningful. These variables represent annual trends in seasonality and extreme or limiting environmental factors (Hijmans et al. 2005). In addition, we included elevation, aspect,

slope and distance to rivers (SRTM Data) for topographical variables. For soil variables, we extracted for each sample point the dry bulk density (Bden), cation exchange capacity (CEC), soil pH measured in H_2O (SpH), soil organic carbon (SOC) and soil organic carbon content (SCC) from Soilgrids database (www.soilgrids.org), a collection of international soil classes and characteristics of the world, based on modern statistical modelling techniques (Hengl et al. 2014). We also considered soil information from a local database (La Araucanía soil series; Pfeiffer et al. (2019)): erodability (value and range), erosion risk, erosion class and evapotranspiration. For anthropogenic variables, we estimated distance to roads, wildfires and agricultural burning (IDE, Minagri https://ide.minagri.gob.cl/geoweb/) and distance to urban centres (i.e. cities and towns). We measure proximity to the main land cover by the Euclidean distance to native forests, forest plantations, agricultural land and pasture covers.

Modelling and predicting IPs community presence and distribution

Our models considered the landscape variables as explanatory (predictor) variables and presence and distribution as response variables (i.e. richness, abundance and basal area of IPs' community). We built a correlation matrix between landscape variables and excluded all highly correlated variables ($|r| > 0.6$) to avoid multicollinearity for model building. We used boosted regression trees (BRT) for statistical modelling, a technique that comprises two algorithms, to link the explanatory variables (landscape variables) to the dependent variables (IPs variables). BRT generates many regression trees combined into one ultimate regression tree model, drastically boosting accuracy and predictive performance (Elith et al. 2008). We generated regression trees using the gbm package in R (Ridgeway 2007). This procedure uses three variables, namely, learning rate (lr), bag fraction (bf) and tree complexity (tc). We built several models using different lr and tc values to obtain the optimal combination (Elith et al. 2008). We reduced the models by removing variables with less relative influence every time we ran them until they had their best performance, represented by a high explained deviance (D^2) and low error (rRMSE). Additionally, the most frequently appearing variables had greater consistency and were eventually selected. After training the model, a validation accuracy score estimates the model performance on an independent dataset (20%). When the dataset of observations is divided into k disjoint subsamples (or folds), then a group is taken as a holdout or test dataset and the remaining groups as a training dataset; this procedure is known as K-fold cross-validation. In our study, we adopted the latter procedure (with K = 5) to validate, avoid overfitting and estimate the average classification.

Then, we calculated the performance for each fitted model (percentage explained deviance; D^2) (Littke et al. 2014), the relative root-mean-square error (rRMSE) (Aertsen et al. 2010) and the correlation between observed and predicted values. We chose those predictor variables with a strong relationship with the response variable (> 10% of influence in BRT models). The model estimates the relative influence of predictor variables (influence) by the frequency at which a variable is selected for splitting, weighted by the squared model improvement due to each split and averaged over all trees (Elith et al. 2008). The relative influence of each variable was scaled so that the sum resulted in 100, with higher values, indicating a more substantial influence. The boosting process involves an iterative step-wise process

of selecting the model with the maximum deviance and the minimum rRMSE at each stage (Elith et al. 2008). Finally, models were used to build prediction maps of the IPs distribution and identify the areas with higher values of IPs abundance, richness and basal area. These areas would represent the best conditions for potential IPs invasion according to the landscape variables.

Akin-Fajiye and Gurevitch (2018) used a boosted regression tree to model factors associated with species presence, density and change in density of an invasive plant. Boosted regression trees are suitable for this analysis because they do not require any assumptions about the data distribution, do not impose linearity and accommodate missing data using surrogates. Nunez-Mir et al. (2019) also used a boosted regression tree to develop a statistical model to predict with 86% accuracy on average the invasiveness of alien woody plant species found across the United States by comparing 63 invasive and 794 non-invasive exotic woody plant species naturalised. The boosted regression tree model comprises a flexible regression structure with improved predictive performance affected by boosting (Colin et al. 2018). Boosting is an adaptive method combining many simple models to improve predictive performance. In their research, Colin et al. (2018) conclude that boosted regression trees are an appealing method for estimating green vegetation from remotely-sensed images. Boosted regression trees benefit from being robust to the inclusion of irrelevant predictors and the presence of outliers (Forsyth et al. 2018). Boosted regression trees can also model complex non-linear relationships, including step-functions and generally predict better than traditional modelling approaches (Elith et al. 2008).

Results

General patterns of species richness

We recorded in the study area a total of 247 plant species, of which 61 (24.6%) were alien species (Appendix 1: Table A2). The proportion between life forms (i.e. tree and shrub) were similar and balanced (circa 1:1) amongst landscapes. However, this ratio varied when considering native or alien species. For native species, trees and shrubs were relatively balanced (56% and 44%, respectively). Meanwhile, of the 61 alien species, most were trees (67%) and the rest were shrubs (33%).

Total native species richness was higher in Pucón (58) and Curarrehue (52) than in Lumaco (39) and Freire (31) (Fig. 3a). The proportion between native and alien species was different amongst landscapes, being highest in the number of alien species in Freire, with 28 out of 59 (47.5%), but ≤ 20% in the other three landscapes. Proportions between life forms (trees and shrubs) were also variable amongst landscapes. We recorded six trees and five shrubs (20%) of alien plants in Lumaco, nine trees and three shrubs (19%) in Curarrehue and seven trees and three shrubs (15%) in Pucón (Fig. 3b).

We found eight invasive species (IPs community) in the study area, meaning 15% of the total alien species in the study area (a total of 61 alien plants) (Fig. 3b): three tree species (*Acacia dealbata*, *Acacia melanoxylon* and *Eucalyptus globulus*) and five shrubs (*Cytisus striatus*, *Rosa rubiginosa*, *Rubus ulmifolius*, *Teline monspessulana* and *Ulex europaeus*). In Lumaco, 64% of alien plants were invasive species. In Freire, 25% of alien plant species were invasive, while in Pucón and Curarrehue, we found 50% and 33% of invasive plant species, respectively.
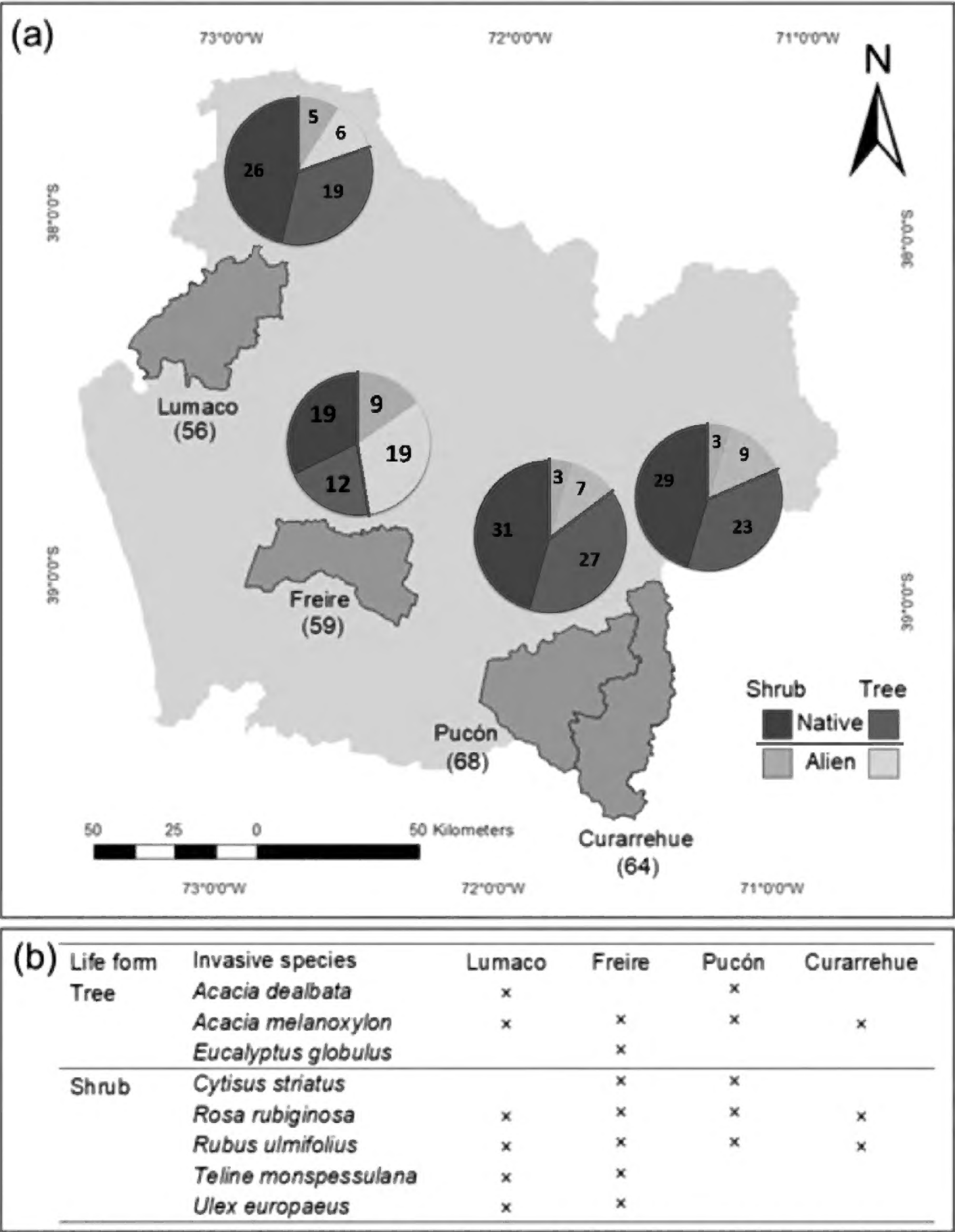
Figure 3. Richness and abundance of invasive plant species in four landscapes in La Araucanía Region, south-central Chile **a** the number of native and alien species by life form. In parenthesis, the total number of species in each county **b** invasive species registered in each county.

Landscape variables influencing the IPs' community

After checking the correlation matrix, the boosted regression tree models and the consistency of explanatory variables of each model (Appendix 1: Table A3), we selected the following variables for the models: 1) distance to forest plantations, 2) distance to towns and populated centres, 3) distance to rivers; 4) the minimum temperature of the coldest month (TMin), 5) cation exchange capacity at 22.5 cm deep (CEC 22.5) and 6) soil organic carbon stock in 15–30 cm depth (SOC). Due to the large number of landscape variables considered, we ran a high number of models (n = 130) with different explanatory variables. Checking for the deviance value and the best performance evaluation allowed us to obtain fewer and better models relying on a few explanatory variables (Table 1). The models with the best performances (best goodness of fit) included the basal area of IPs' trees, IPs' abundance and IPs' richness, respectively.

Table 1. Performance statistics for boosted regression tree models of invasive plants species using three indicators (species richness, abundance and tree basal area). Explained deviance of the fitted model (D^2), Pearson's correlation coefficient (corr) and relative root mean square error (rRMSE) are reported. * Values for cross-validation.

Model	D^2	D^2 cv*	Corr	Corr cv*	rRMSE*
Tree basal area	0.97	0.68	0.98	0.66	9.04
Abundance	0.57	0.35	0.71	0.59	14.88
Richness	0.49	0.32	0.72	0.57	21.01

Modelling IPs community distribution

Distance to forest plantations was the primary explanatory variable in all models (Fig. 4). This explanatory variable had the strongest relative influence on species richness, abundance and basal area of invasive trees, overcoming 50% of relative influence and reaching a maximum of 85%. For IPs richness, distance to forest plantations had 57.5% of the relative influence, while soil organic carbon stock and distance to towns were the second and third variables, with 26.5% and 16%, respectively (Fig. 4a). For IPs abundance, distance to forest plantations had 85% of relative influence. In contrast, cation exchange capacity (CEC22.5) distance to populated centres were the second and third variables, with 8% and 7%, respectively (Fig. 4b). For the basal area of IPs trees, distance to forest plantations was 59% relative influence; the minimum temperature of the coldest month (TMin) and the distance to rivers were the second and the third variables, with 22% and 20%, respectively (Fig. 4c).

Partial dependence plots showed that the less distance from the forest plantations, the greater the IPs richness and abundance and basal area of IPs trees (Fig. 5a). All these explanatory variables showed a striking decrease of around 1000 m to forest plantations. Soil organic carbon stock and distance to towns also appeared as explanatory variables in the species richness model. IPs richness kept constant with soil organic carbon stock until it almost attained 60 tonnes per hectare, then it fell abruptly (Fig. 5b). IPs richness also increased along with the distance to towns up to around 10,000 m and decreased gradually. IPs' abundance constantly decreased along with increased cation exchange capacity (CEC 22.5 deep), with a sudden fall when this explanatory variable reached 30 cmolc/kg. IPs also decreased further from cities. The basal area of IPs' trees was higher near forest plantations; the striking decrease occurs before 500 m distance (Fig. 5c). The basal area remained constant with low values of the minimum temperature of the coldest month (TMin), but increased just when this temperature surpasses 3.8 °C. The relationship between the basal area of IPs' trees and distance to rivers was irregular, decreasing the basal area through increased distance to rivers.

Predicting the IPs community distribution

Distribution models predicted higher IPs' richness in Lumaco than in the other landscapes (Fig. 6a), especially in the northern area. In Freire, the highest IPs' richness was predicted alongside the Allipen River (which crosses the territory) and a tree plantation patch. Meanwhile, in Pucón and Curarrehue, models predicted only small patches of higher IPs' richness. Regarding IPs' abundance (Fig. 6b), in Lumaco, landscape variables enhance the highest abundance of IPs in practically
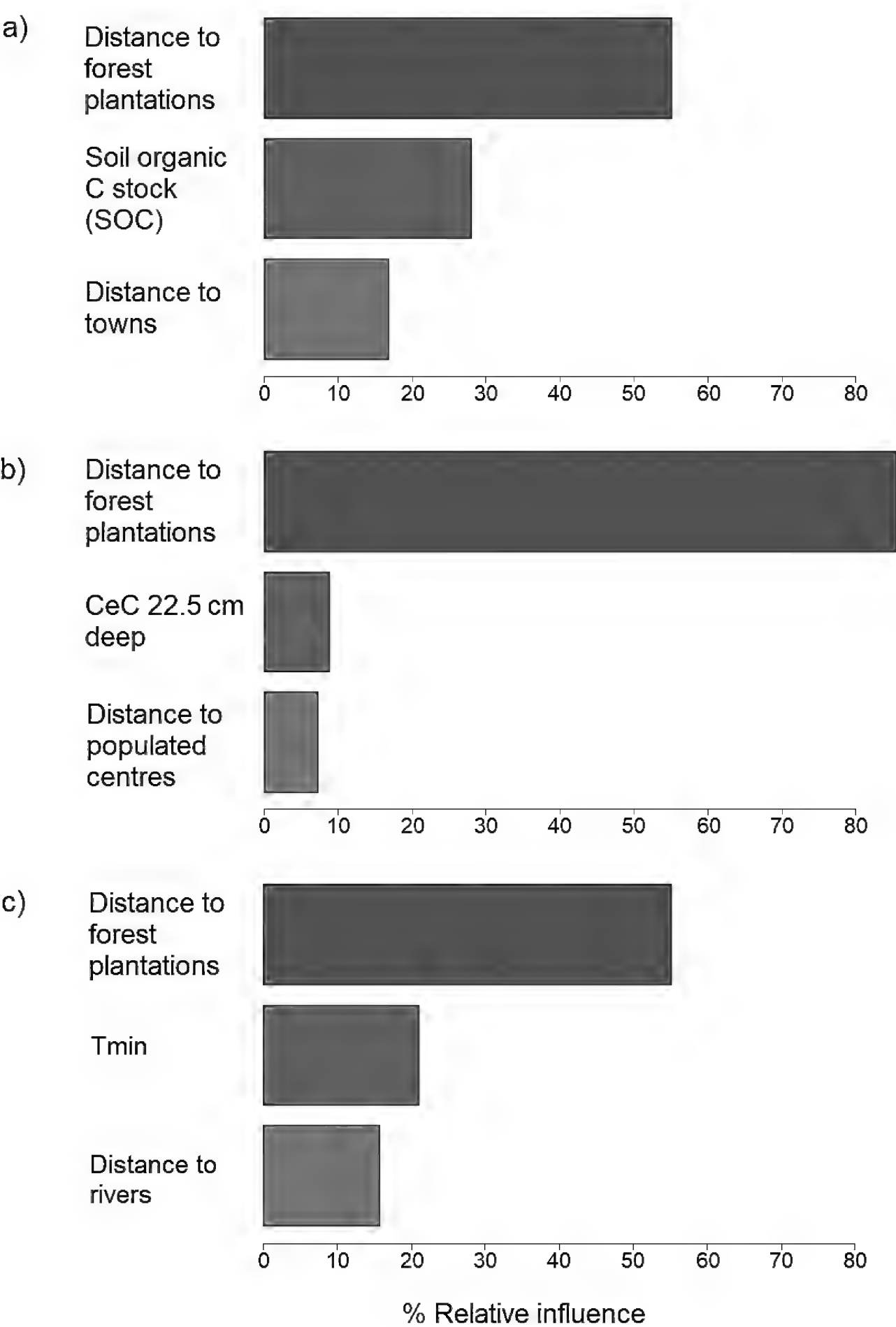
Figure 4. The relative influence of landscape variables in boosted regression tree models of invasive plant species **a** richness **b** abundance and **c** tree basal area. Explanatory variables include distance to forest plantations, towns, populated centres and rivers, minimum temperature of the coldest month (TMin), cation exchange capacity (CEC22.5) and soil organic carbon stock.

the entire county. In the other landscapes, the highest abundance coincides with the patches observed for the richness model. We found the highest basal area values of invasive trees in Lumaco (Fig. 6c), but basal area varied more than abundance values. There were small patches with high basal area values in the other landscapes. but to a lesser extent than richness and abundance. IPs' richness, abundance and the basal area of trees had similar spatial patterns; therefore, areas of higher IPs' invasion risks in the study area coincided for all models, although they included different explanatory variables. Boosted regression tree model predictions showed that Lumaco is the county with the highest probability of spreading invasive plants, while Curarrehue has the lowest probability.
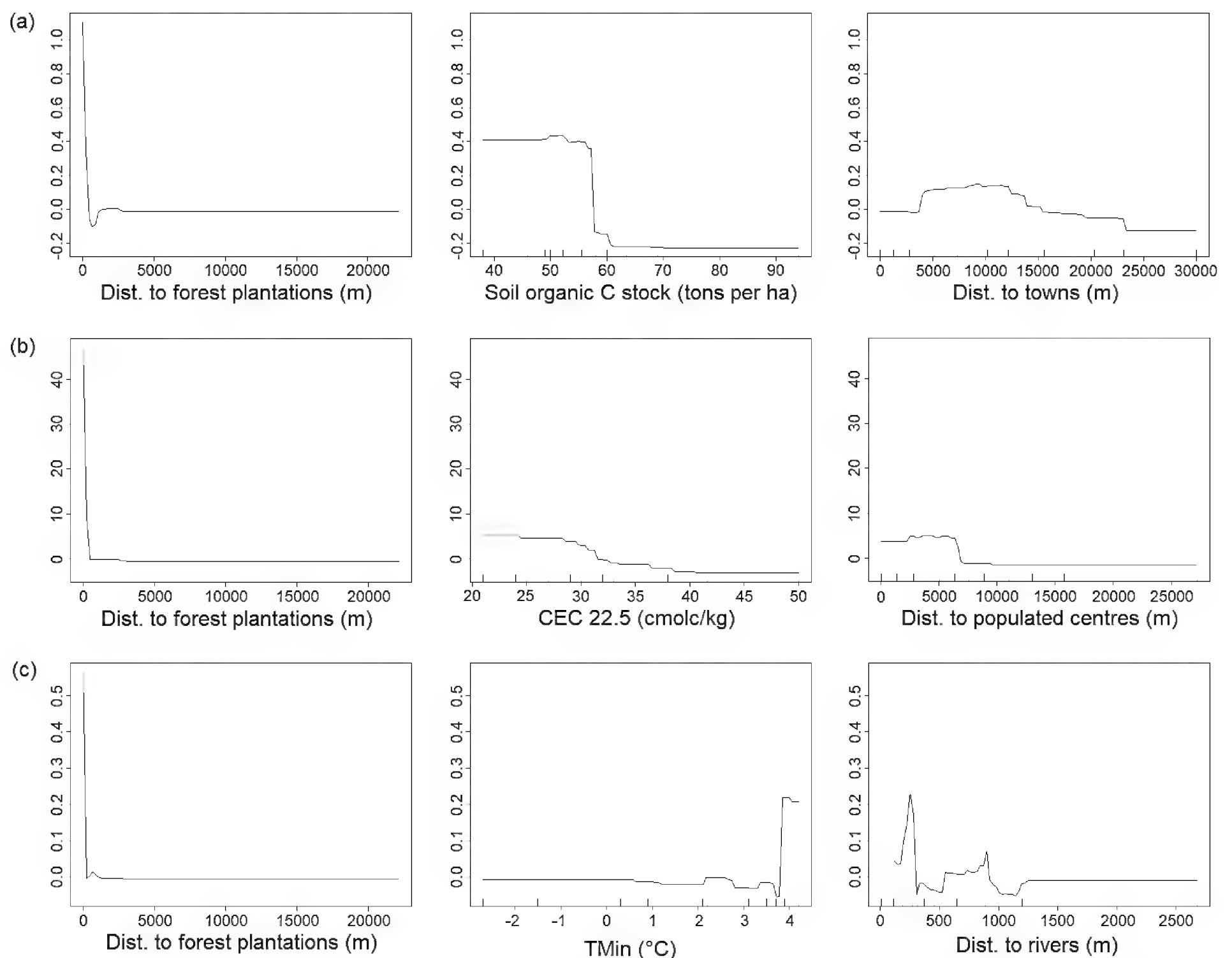
Figure 5. Partial dependence plots for the three most influential variables on IPs' richness (**a**), abundance (**b**) and basal area of trees (**c**). Y-axes in logit scale and centred on a zero mean over the data distribution. Interior marks show deciles across the Y-axes.

Discussion

Landscape variables influencing the IPs community

Proximity to forest plantations resulted in the primary landscape variable influencing IPs' distribution. Recent reviews have shown that forest plantations are generally related to lower local species richness than native ecosystems (Escobedo et al. 2017; Brazeiro et al. 2018). In some cases, substituting native ecosystems with forest plantations reduced local plant richness by an average of 35% (Brazeiro et al. 2018). Disturbance often drives plant invasion and may modify the community assembly (Escobedo et al. 2017). Disturbance events (e.g. fire, grazing, mowing activity of fossorial mammals and tree plantation conversion) remove plant biomass and create invasive plant species colonisation (Mouillot et al. 2013). IPs' frequently grow faster than natives, have more efficient seed dispersal and higher resource-use efficiency and fecundity than native species (Van Kleunen et al. 2010); thus, they can rapidly colonise and establish disturbed sites.

Changes in land use and land cover may result in spatial shifts in the invasion risk of IPs (Wang et al. 2016). The invasive plant usually establishes when a disturbance such as land-use change occurs. The landscape permeability increases, allowing colonisation by the invasive plant and producing patchily distributed stands of the same
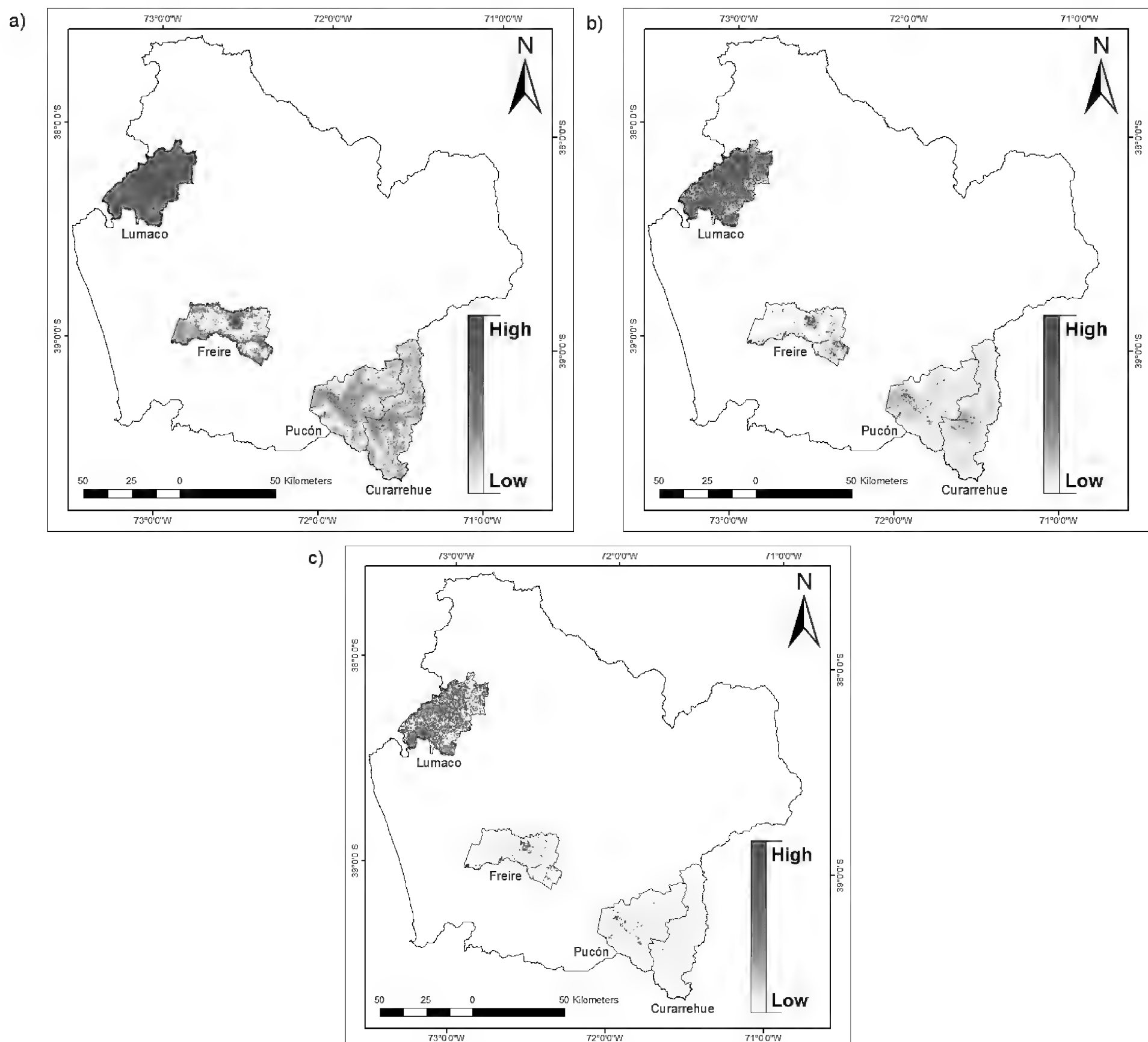
Figure 6. Predictions for IPs' community distribution for species richness (**a**), abundance (**b**) and (**c**) basal area of invasive trees.

age. Many IPs perform better in cleared areas; thus, the connectivity of cleared areas is as critical for colonisation as the connectivity of undisturbed habitats (Green et al. 2006). One rule of thumb in invasion biology mentions "that land use promotes invasions" and might be reversed in many landscapes; for example, land management can form an invasion barrier, whereas land abandonment often enables invasion (Kueffer 2017). For example, high agricultural labour and intense grazing may temporarily "control" tree and shrub invasions (*Rubus ulmifolius*, *Ulex europaeus*, *Acacia* spp). However, it does not imply that those species cannot re-invade after land abandonment or if the land is converted to forest plantations. Selective grazing pressure by livestock, whereby the animals selectively seek the more palatable species first or exclusively, can create an environment conducive to IPs (Morokong and Blignaut 2020).

High values of IPs' richness, abundance and tree basal area were recorded near forest plantations. For the implementation of forest plantations, planting, pruning and thinning activities are carried out in the first years with the application of pesticides. These tasks involve the removal of the original vegetation, the alteration

of both the soil structure and water regulation (Granados-Sánchez et al. 2007; Jullian et al. 2018; Gómez 2021). This generates a scenario of opportunities for new spaces for the entry of IPs. Studies indicate that the invasion of species such as *Ulex europaeus* has been strongly influenced by landscape context and dynamics, particularly in land covers, such as forest plantations (Altamirano et al. 2016). It reinforces findings from studies in Mediterranean landscapes showing that landscape composition (land use/cover) represents by far the most important group of variables associated with invasions of alien plant species (González-Moreno et al. 2015). IPs are taking advantage of niches available in more open and degraded land covers, such as bare land, agriculture and shrublands (Altamirano et al. 2016). Thus, it is expected that alterations and change dynamics constitute ideal scenarios for establishing invasive species, taking advantage of disturbed or deforested areas and over-grazed meadows. It is essential to recognise the role of linear corridors, such as roads, canals and abandoned lots, like reservoirs and conduits for the movement and re-invasion of invasive plants in the landscape. For example, in our study area, these strips usually contain several herbaceous shrubs and tree species that can survive there because disturbance occurs at a much lower frequency than in the agricultural field. In contrast, some areas have fences that reduce domestic grazing.

A higher basal area of invasive trees near rivers might be related to the basic need for water and the reduced competition from native plants due to regular flooding (Čuda et al. 2017). In the first metres, the rocky riverbed prevents the establishment of these plants. Models predicted the highest basal area values of IPs' trees in the most stable and consolidated riverside area. Rivers may act as a source of IPs' propagules (Chytrý et al. 2008; Catford et al. 2011), thus serving as a dispersal pathway for a high species number (rivers are of the most invaded ecosystems globally). The irregular trend found for the relationship between rivers and the basal area of IPs' trees seen could be based on the topographical profile of areas surrounding rivers and anthropogenic interventions such as roads, forest plantations and agricultural land. Finally, we can add landscape fragmentation; in Chile, the Mediterranean ecosystems of the central zone are the areas most affected by habitat loss and fragmentation in the country (Blondel and Fernández 2012), reducing vegetation to patches. The minimum temperature of the coldest month showed a direct relationship with the basal area of invasive trees. Invasive species require moderate temperatures in the coldest month to maintain their productivity. In temperate climates, most invaded areas by alien plants correspond to higher annual average temperatures and low altitudes, making these areas environmentally more favourable (González-Moreno et al. 2015).

Invasive species richness also indicates key ecosystem services such as carbon storage. For instance, values are higher at a range of 38 to 58 tonnes per hectare of soil organic carbon content; under this interval, there are no data. An adequate amount of soil organic carbon content is essential for sustainable agriculture and mitigating C flux to the atmosphere (Yimer et al. 2006). A decline in SOC generally decreases vegetational productivity and alters the soil's capacity to act as a sink for atmospheric CO_2.

Modelling IPs' distribution

The basal area of invasive trees resulted in the best model to predict IPs' community distributions. Distance to forest plantations, minimum temperature of coldest month and distance to rivers were the main explanatory variables of this model. These variables express the disturbance, climatic condition and water availability of the study

area. Tree basal area is frequently used as an indicator of the condition of tree cover and to evaluate the effect of different phenomena and processes, such as climate change, invasion, forest inventories and restoration (Bradford and Bell 2017; Jo et al. 2018; Suganuma et al. 2018; Corona et al. 2019). Tree basal area is also an indicator of forest recovery and it is amongst the structural attributes suggested as a reference for monitoring restoration projects (Suganuma et al. 2013; Altamirano et al. 2019). Structural attributes are measurable even in the early stages of community development, which places them as good indicators for monitoring the evolution of communities. Basal area values may indicate the incorporation of biomass by the species used in the restoration process with the influence of density (dos Reis et al. 2014). Additionally, there is a relationship with habitat quality since basal area shows the highest values in places with adequate climatic, soil and biotic conditions. Tree basal area has a rapid increase when it is favoured by conditions of high availability of light, the proximity of watercourses and nutrients, which is a fundamental feature for its recommendation as a monitoring indicator and reference values as possible targets for restoration. Londe et al. (2020) considered basal area amongst eleven ecological indicators commonly used to evaluate the monitoring and evaluation of restoration forests. These researchers ratify that these indicators are also suitable for monitoring reference ecosystems of different dimensions since the mature fragments did not influence them. The basal area had a significant relationship with the fragment area. However, we also need to consider some limitations of model predictions (Jarnevich et al. 2015). For instance, the number of samples will be usually desirable, being as large as possible, but it also depends on financial resources. Some context variables are unavailable, but can be useful to explain the variation and distribution of IPs (e.g. social variables). Therefore, uncertainty is part of model inference and a important topic to consider. Our approach has limitations, but is a useful tool to guide management decisions to control IPs.

Predicting the IPs' community distribution

Our models represent introduced organisms that managed to naturalise, establish successfully and disperse widely, occupying environments with a wide variety of climatic, topographical, soil qualities and anthropogenic intervention. Therefore, our prediction models would be more accurate to represent reality. Perret et al. (2019) suggested that the distribution modelling of invasive plants focusing solely on the conditions experimented in the range and native region of a species may be misleading. For example, the genus *Pinus* L. has shown an increase in its niche size by 10% in territories that invade worldwide from its niche size in its place of origin (Perret et al. 2019). These species show great physiological capacities to grow in more diverse and extreme climatic conditions than in their original distribution range. Besides, in their new territories, IPs occupy a niche broader than their original one due to the release from some of the constraints in their territory (such as predators, diseases and parasites) (Guisan et al. 2014; Tingley et al. 2014; Perret et al. 2019).

Boosted regression tree model predictions for the basal area of IPs trees showed a significant relationship between a larger basal area of invasive trees and sites where land use is mainly forest plantations and close to rivers, as occurs in Lumaco. As the most disturbed one (i.e. with the most extensive replacement of native vegetation by forest plantations), this county showed the highest probabilities of IPs' invasion risk. Pucón and Curarrehue, on the opposite extreme of the disturbance gradient, showed the lowest probability values.

The predictions of our models, based on local information, can give early detection of the areas with a higher probability of being colonised by invasive plant species. This would allow government agencies and land managers to respond rapidly to prevent invasive plants from thriving in new environments following their introduction (Battini et al. 2019). Species distribution models are widely used to predict the potential distribution of invasive species, providing excellent tools for designing strategies to prevent or mitigate impacts of alien invasive species. Our predictions can also guide management under a global change scenario.

Our models can be suitable tools for designing strategies to prevent, mitigate or make integrated control of the impacts of invasive species. For example, in Pucón and Curarrehue, strategies based on our inferences and predictions would be helpful to prevent invasion of the protected areas: Huerquehue National Park, Villarrica National Park and Villarrica National Reserve (CONAF 2011). Furthermore, knowing the richness, abundance and distribution of alien species provides essential information to design prevention activities, early detection and integrated control of invasive alien species within protected areas. These actions are being considered urgent globally to ensure the conservation of native flora (Kutschker et al. 2015). On the other hand, our models could be used to mitigate the impact of invasive plant species in Lumaco and Freire and they can even be considered in native forest restoration programmes.

Conclusions

Land use is a critical landscape variable influencing the presence and distribution of the community of invasive plants. In particular, proximity to forest plantations was the most influential variable in all models.

Even IPs occupy human-disturbed environments since these types of interventions enhance biological invasion; we do not know the main factors that allow the invasion's success in anthropogenised temperate environments with high accuracy. We hope our findings will help increase knowledge about the landscape characteristics that influence invasion processes, understand what promotes species invasion outside their natural range and predict which ecosystems will be invaded and under what conditions. In this way, decision-makers could act in time to implement prevention, mitigation and restoration measures against invasions of alien plants, especially in high-diversity places, such as protected areas and sites that deliver ecosystem services.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Author contributions

Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data Curation, Writing, Funding Acquisition; Juan Gutiérrez: Methodology, Formal analysis, Investigation, Resources, Data Curation, Writing; Adison Altamirano: Conceptualization, Investigation, Resources, Data Curation, Writing, Funding Acquisition; Aníbal Pauchard: Conceptualization, Methodology, Writing; Paula Meli: Conceptualization, Methodology, Writing.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Appendix 1

Table A1. Biophysical characteristics of study area.

Municipality	Lumaco	Freire	Pucón	Curarrehue
Climate (Ministerio de Agricultura 2015)	Warm temperate rainy with Mediterranean influence	Warm temperate rainy with Mediterranean influence	Warm temperate with Mediterranean influence and to a lesser extent cold rainy temperate with Mediterranean influence and tundra due to the effect of altitude.	Cold rainy temperate with Mediterranean influence and in lesser medium tundra due to the effect of altitude and warm temperate with Mediterranean influence.
Average annual temperature (°C) (Hijmans et al. 2005)	10.94	12.07	8.62	7.69
Mean maximum temperature warmest month (°C) (Hijmans et al. 2005)	23.7	24.66	22.63	22.11
Mean minimum temperature coldest month (°C) (Hijmans et al. 2005)	2.78	3.75	0.07	-1.08
Average rainfall of the wettest month (mm) (Hijmans et al. 2005)	228.97	266.93	294.2	227.52
Average rainfall of the driest month (mm) (Hijmans et al. 2005)	26.66	40.98	45.27	31.35

Table A2. Plants species in four landscapes of La Araucanía Region, south-central Chile.

Life form	Species	Study area			
		Lumaco	Freire	Pucón	Curarrehue
Native species					
Tree	*Araucaria araucana*				X
	Austrocedrus chilensis				X
	Aextoxicon punctatum	X	X	X	X
	Amomyrtus meli			X	
	Amomyrtus luma	X			
	Cryptocarya alba	X			
	Caldcluvia paniculata			X	
	Dasyphyllum diacanthoides	X		X	X
	Drimys winteri	X	X	X	X
	Embothrium coccineum	X	X	X	X
	Eucryphia cordifolia	X	X	X	X
	Gevuina avellana	X		X	X
	Lithraea caustica	X			
	Lomatia hirsuta	X	X	X	X
	Luma apiculata	X	X	X	X
	Laureliopsis philippiana			X	X
	Laurelia sempervirens	X		X	X
	Luma chequen			X	
	Myrceugenia planipes			X	
	Maytenus boaria	X	X	X	X
	Myrceugenia exsucca		X	X	X
	Nothofagus alpina	X	X	X	X
	Nothofagus dombeyi	X	X	X	X
	Nothofagus antarctica			X	X
	Nothofagus oblicua	X		X	X
	Nothofagus pumilio			X	X
	Peumus boldus	X	X	X	
	Persea lingue	X	X	X	X
	Podocarpus nubigenus			X	
	Podocarpus saligna	X			X

Life form	Species	Study area			
		Lumaco	Freire	Pucón	Curarrehue
Tree	*Saxegothaea conspicua*			X	X
	Sophora cassioides			X	
	Weinmannia trichosperma			X	X
Shrub	*Aristotelia chilensis*	X	X	X	X
	Azara dentada	X		X	X
	Azara lanceolata		X	X	
	Azara serrata	X	X	X	X
	Azara integrifolia	X	X	X	
	Azara microphylla		X	X	X
	Baccharis concava	X			
	Berberis darwini	X	X	X	X
	Baccharis racemosa	X			X
	Baccharis poeppigiana	X			
	Buddleja globosa			X	X
	Berberis empetrifolia			X	
	Baccharis linearis	X			
	Berberis microphylla			X	X
	Berberis negeriana				X
	Berberis rotundifolia	X			X
	Berberis trigona			X	X
	Chusquea culeou	X	X	X	X
	Colletia spinosa	X		X	X
	Chusquea quila	X	X	X	X
	Colliguaja salicifolia				X
	Cynanchum pachyphyllum			X	
	Drimys andina			X	X
	Discaria serratifolia		X		
	Desfontainia spinosa			X	X
	Ephedra chilensis	X			
	Fuchsia magellanica		X	X	
	Gaultheria mucronata	X	X	X	X
	Gaultheria pumila			X	
	Greigia sphacelata		X		
	Loasa acanthifolia				X
	Lomatia dentata	X	X	X	X
	Lomatia ferruginea			X	
	Lapageria rosea	X	X	X	
	Myrceugenia chrysocarpa				X
	Maytenus disticha			X	X
	Muehlenbeckia hastulata		X		
	Mitraria coccinea			X	
	Maytenus magellanicus			X	X
	Myrceugenia lanceolata			X	
	Myrceugenia parvifolia				X
	Myrceugenia leptospermoides	X			
	Ovidia andina	X			
	Piper aduncum		X		
	Psoralea glandulosa		X		
	Pseudopanax laetevirens	X		X	X
	Rhamnus diffusus	X			
	Ribes magellanicum	X		X	X
	Rhaphithamnus spinosus	X	X	X	X
	Sophora macrocarpa	X			
	Sphacele chamaedryoides	X			
	Ugni molinae	X	X	X	
	Vestia foetida				X

Life form	Species	Study area			
		Lumaco	Freire	Pucón	Curarrehue
Alien species					
Tree	*Acacia dealbata*	X		X	
	Acacia melanoxylon	X	X	X	X
	Acer pseudoplatanus		X		X
	Betula sp		X		
	Castanea sativa			X	X
	Corylus avellana		X		X
	Crataegus monogyna	X			
	Cupressus macrocarpa	X	X	X	
	Eucalyptus delegatensis		X		
	Eucalyptus globulus	X	X		
	Eucalyptus nitens		X		X
	Laurus nobilis		X		
	Malus domestica		X	X	X
	Pinus radiata	X	X	X	X
	Populus alba		X		
	Prunus cerasus		X		
	Prunus domestica		X		
	Prunus pérsica		X		
	Pseudotsuga menziesii		X	X	X
	Quercus ilex		X		
	Quercus petraea		X		
	Quercus Rubur				X
	Salix babylonica				X
	Sequoia sempervirens		X		
Shrub	*Acacia farnesiana*		X	X	
	Cytisus striatus	X	X	X	
	Rosa rubiginosa	X	X	X	X
	Rubus ulmifolius	X	X	X	X
	Salix caprea		X	X	
	Salix viminalis		X	X	
	Smilax aspera		X	X	
	Teline monspessulana	X		X	
	Ulex europaeus	X	X	X	
	Vaccinium myrtillus		X	X	

Table A3. Consistency and frequency of explanatory variables of each model.

Response variable	Explanatory variable	Consistence	Frequency	Mean relative influence (%)
Richness	Dist. to forest plantations	1.0	12	48.9
	Soil organic C stock	1.0	12	24.5
	Dist. to towns	1.0	12	15.2
	Dist. to agric. land	0.9	11	9.7
	Dist. to populated centres	0.8	10	7.4
	Dist. to agric. burning	0.8	9	7.3
	Temp. annual range	0.7	8	6.5
	Dist. to prairies	0.6	7	4.9
	Cation exchange capac. (15 cm)	0.5	6	4.1
	Soil org. C content (30 cm)	0.4	5	3.8
	Bulk density (15 cm)	0.3	4	3.3
	Dist. to forests fires	0.3	3	2.4
	Aspect	0.2	2	1.4
	Mean diurnal range temp.	0.1	1	0.9
Abundance	Dist. to forest plantations	1.0	9	86.3
	Cation exchange cap. (22.5 cm)	1.0	9	7.5
	Dist. to populated centres	1.0	9	5.6
	Soil organic C stock	0.9	8	4.9
	Dist. to cities	0.8	7	4.2
	Dist. to native forest	0.7	6	3.9
	Slope	0.6	5	3.1
	Bulk density (15 cm)	0.4	4	2.6
	Aspect	0.3	3	2.7
	Dist. to prairies	0.2	2	1.6
	Elevation	0.1	1	0.3
Invasive Tree basal Area	Distance to forest plantations	1.0	15	53.4
	TMin	1.0	15	13.5
	Dist. to rivers	1.0	15	11.0
	Dist. to native forest	0.9	14	9.3
	Precipitation Seasonality	0.9	13	6.7
	Dist. to prairies	0.8	12	6.6
	Soil org. C content (30 cm)	0.7	11	4.9
	Dist. to populated centres	0.7	10	3.8
	Bulk density (15 cm)	0.6	9	2.4
	Dist. to roads	0.5	8	2.1
	Soil organic C stock	0.5	7	1.0
	Soil org. C content (15 cm)	0.4	6	0.6
	Dist. to cities	0.3	5	0.5
	Dist. to agric. burning	0.3	4	0.4
	Soil org. C content (22.5 cm)	0.2	3	0.4
	Dist. to forests fires	0.1	2	0.3
	Soil pH × 10 in H_2O (30 cm)	0.1	1	0.1